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- Wavelength Categorization by Goldfish**
(Carassius auratus) 195
Marjorie Goldman, Robert Lanson,
and Gabriela Rivera
- Dominance Behavior in Asexual Gecko,**
Lepidodactylus lugubris, and its
Possible Relationship to Calcium 211
Susan G. Brown, Linda K. Osbourne,
and Maile A. Pavao
- Boxing in Red Kangaroos, Macropus Rufus:**
Aggression or Play? 221
David B. Croft and Fiona Snaith

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WAVELENGTH CATEGORIZATION BY GOLDFISH (*CARASSIUS AURATUS*)

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ABSTRACT: Goldfish pressed a paddle for intermittent food reinforcement in the presence of one of seven different monochromatic wavelengths. Wavelengths in 20 nm steps from 430 to 690 nm, matched for "brightness," were then presented for 20 days during which food maintained responding to the training stimulus. Generalization gradients calculated from the final four days were asymmetric. A long wavelength gradient showed maintained responding above 630 nm; at short wavelengths responding generalized below 490 nm; four middle wavelength gradients could indicate two groupings having maximum responses at around 510 and 570 nm.

The physiology of the goldfish visual system has been extensively described (Wheeler, 1982). The three cone pigments are maximally sensitive to wavelengths of 455, 530, and 625 nm (Marks, 1965; Harosi and MacNichol, 1974). In the subsequent stages of retinal processing there are cells which respond in an opponent fashion. Some horizontal cells hyperpolarize and depolarize to different wavelengths (MacNichol and Svaetichin, 1958; Tomita, 1965); many bipolar and amacrine cells are color-coded (Kaneko, 1973); there are ganglion cells with double-opponent receptive fields (Daw, 1968; Spekrijse, Wagner, and Wolbarst, 1972; Beauchamp and Lovasik, 1973; Mackintosh, Bilotta, and Abramov, 1987); and single cells in the optic tectum of the goldfish respond in an opponent manner (Jacobson, 1964). In addition to these physiological descriptions, what is needed is an understanding of how this information is integrated and used by the fish.

This paper examines how the various wavelengths are grouped together by the goldfish. This issue has been explored in nonhuman animals in two ways: matching-to-sample and generalization gradients. Wright and Cumming (1971) described "color-naming" gradients for pigeons using a matching-to-sample technique. After the pi-

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geons were matching three different wavelengths with 90% accuracy, sample probes of wavelengths in between the original training stimuli were presented. The pigeons had to respond to nonmatching hues on the side keys as if they were a match. The three functions derived from the data had transition points at 540 and 595 nm. These groupings are different from human color naming functions where transitions occur around 492, 561, and 605 nm (Boynton and Gordon, 1965). The application of this method to goldfish is complicated by the fact that on matching-to-sample tasks goldfish do not reach the high levels of accuracy needed for reliable assessment of "color-naming" transition values (Goldman and Shapiro, 1979).

Generalization gradients are obtained by presenting a series of unreinforced wavelengths after the animal has been trained to respond to one wavelength. Usually the animal is reinforced on a variable interval schedule during training to ensure a steady response rate. If tested in extinction, the animal gradually stops responding during a single session so that few responses are made to stimuli presented at the end. To maintain responding during the testing phase, Blough (1961) obtained steady state generalization gradients from his pigeons by reinforcing responses during four of the six presentations of the training stimulus which were interposed among many other unreinforced wavelengths. The reinforced stimulus was changed every few days so that over the course of the study each bird was successively tested for generalization to a number of different wavelengths. Although the results showed the effects of previously reinforced wavelengths and individual idiosyncracies, Blough found consistent asymmetries in the shapes of the gradients. A symmetrical gradient shows responses tapering off equally at both higher and lower wavelengths around the training stimulus, suggesting that the training stimulus is located in the middle of a color category. An asymmetrical gradient shows a rapid decline in responding on one side of a specific training stimulus and a more gradual decline on the other side, suggesting that the training stimulus is located closer to one color boundary. For all of Blough's birds, a rapid decline occurred at 540 nm, in agreement with the data from Wright and Cumming, while two out of four birds showed a steep gradient at 590 nm. Emmerston (1983) has summarized results from wavelength discrimination experiments on pigeons and has shown a high degree of correspondence among data obtained with steady state generalization gradients, matching-to-sample, and hue discrimination procedures.

Two wavelength generalization gradients have been obtained from goldfish by Yarczower and Bitterman (1965) without controlling for "brightness." One curve shows an almost symmetrical gradient around a 550 nm training stimulus with responses slowing at 490 and 610 nm. The other curve is an asymmetrical gradient around a 580

nm training stimulus where the peak is shifted to 560 nm, responding is still high at 520 nm, and there is a steep decline at 620 nm. The small number of gradients and the narrow range of spectral values explored make it difficult to assess color categorization in the goldfish. In the present experiment the fish were tested using a reinforced generalization procedure similar to Blough's, but more training and testing sessions were added to try to lessen the effects of previous wavelength training. We used seven different training wavelengths equated for "brightness" and the testing stimuli ranged from 430 to 690 nm to explore more of the spectrum.

METHOD

Subjects

Ten goldfish, 8-12 cm standard length, purchased from a local pet store, were housed individually in 9.6 liter tanks ($31 \times 16.5 \times 20.5$ cm) continuously aerated through plastic filters. The room temperature was maintained at 21° C. Fluorescent room lights were on for 18 h, beginning at 7 am, and off for 6 h. The fish were fed once daily during testing.

Apparatus

The fish tank, with filter removed and debris siphoned, was placed into a black Plexiglas chamber through a hinged side door along the 31 cm side. A single Plexiglas disc, 3.1 cm in diameter, suspended on a steel rod could be lowered into the tank in front of a single hole in one 16.5 cm wall by closing a top lid. The steel rod was suspended from a mechanical relay contact. A sheet of painted black metal extended 8.5 cm below the lid to prevent the fish from hitting the rod. Food pellets were delivered from a tube by a Gerbrands feeder through a 2.5 cm hole 4.75 cm from the black sheet. Mouth press responses to the Plexiglas disc closed the relay contact and were recorded on relay equipment.

Light from a GE tungsten ribbon filament 6 volt bulb passed through heat absorbing glass and was then projected through a Diffraction Products Czerny-Turner grating monochrometer. The monochromatic output could be intercepted by a shutter mounted on an electromechanical positioning motor, which controlled the presentation of the visual stimuli with onset and offset of less than 100 ms. The unblocked monochrometer output was brought to a focus. A Kodak continuous 15 cm diameter circular neutral density absorbing wedge with a mechanical compass along the outer edge was placed in

the focal plane so that the intensity values could be set manually. Light passing through the filter was focused on a ground glass mounted in front of the 3 cm circular hole at the end of the experimental chamber. Fourteen wavelengths (half-band width = 16 nm) ranging from 430 to 690 nm in 20 nm steps were used in testing. These values were manually adjusted between stimulus presentations.

Calibration

The wavelength vernier of the monochromator was calibrated several times during the course of the experiment with a mercury vapor lamp at 546 and 579 nm. Stimulus intensity values were determined based on an average relative spectral sensitivity function as determined for Yager's (1967) data for light adapted goldfish. The points were connected and interpolated values for the wavelengths used were determined. Stimulus value determinations and calibrations were done with an EG and G Model 580/585 radiometer with a photomultiplier head. A computer program determined the radiometric output inversely weighted by the fish sensitivity function (taking into account the spectral sensitivity of the photomultiplier as calibrated by EG and G against a National Bureau of Standards standard). Given the relatively high fish sensitivity in the blue spectral region and the lower output of the tungsten source in that region, an attempt was made to achieve the highest intensity output possible from the system with all stimuli equated for the fish sensitivity. A maximum intensity output was determined for the lowest wavelength value used and the computer determined the outputs required for all other wavelengths. These values were manually set by positioning the wedge to produce the closest approximation to the computer value within accuracies of 3 percent. Radiometric energy levels at 450, 530, and 630 nm were 11.5, 12.0, and 12.2 log quanta/s/square centimeter respectively. These values are comparable to those used by Powers (1978).

Procedure

Each fish was shaped to press the lighted disc with its mouth for Noyes formula "J" 20 mg fish pellets. The disc was transilluminated with one of the testing wavelengths at the appropriate intensity setting. Three fish were initially trained in the presence of 450 nm, three with 530 nm, three with 570 nm, and one with 630 nm. This monochromatic light was the only illumination in the box. After shaping, a random interval (RI) schedule of food reinforcement was instituted and the mean time interval was gradually lengthened until

its final average value of RI 133 s. In this schedule, the first mouth press in a 2 s repeating time period has a .015 probability of earning a Noyes pellet. Subsequent responses in that period are not reinforced. Stimulus light on periods were gradually reduced from 10 min to 2 min. A 15 s blackout followed all stimulus presentations. By the end of approximately 40 days of training, each fish responded at a steady rate throughout the hour and earned about 20 food pellets. Generalization testing involved 2 min presentations of the 14 different stimuli so that each stimulus was presented three times over two days. Reinforcement was programmed to occur on an RI 27 s schedule during six additional presentations of the training stimulus on each day. This schedule permitted approximately the same daily number of food pellets as in the final training conditions. Thus, an example of one day's testing would be 27 light on periods which included 6 of the training stimulus with reinforcement possible, one or two with the training stimulus and no reinforcement possible, and the other 19 periods with the other 13 stimuli presented once or twice, without reinforcement possible. The order of stimulus presentation was determined by random permutation. In the second half of the experiment, a constraint was added that a given wavelength could not follow the reinforcement period more than once. Testing continued for either 20 or 25 days, after which most of the fish were reinforced on an RI 133 s schedule for responding to a new training stimulus. This second training stimulus was presented alone for 10 or 20 days before the generalization testing phase was begun and carried out in the same manner as described for the first training stimulus. After generalization testing, some of the fish were trained and tested on a third stimulus. The following sequences of training stimuli were used for different groups of fish: 450, 530, 630 nm; 530, 590, 490 nm; 570, 510 nm; and one fish was trained to only 630 nm to replace an animal from the first group that had died. For the groups begun with 530 and 570 nm, training time to the second and third stimulus was reduced from 20 days to 10 and testing time for all stimuli was reduced from 25 days to 20 because the shorter time was sufficient to obtain peaked gradients.

RESULTS

The first gradients obtained after single stimulus training to 450 nm, 530 nm, and 630 nm were flat across the wavelength spectrum. The fish trained to 570 nm and one fish trained to 450 nm showed peaked gradients from the first two generalization sessions. Many of the first gradients for the second and third training stimuli showed responses to the previous stimuli. By the 15th to 20th generalization

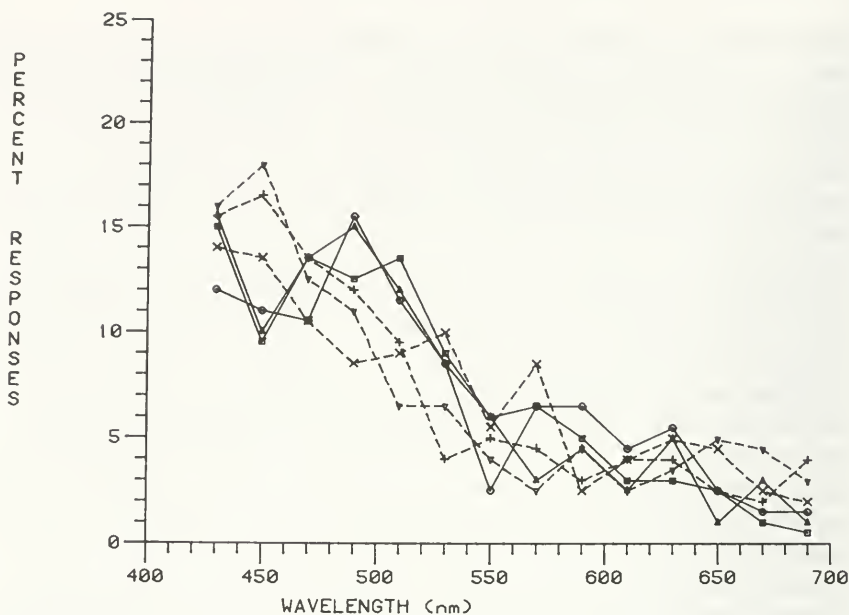


FIGURE 1. Generalization gradients after training to 450 nm (dashed lines) and 490 nm (solid lines) for six different fish from testing days 18-21 (450 nm) or 17-20 (490 nm).

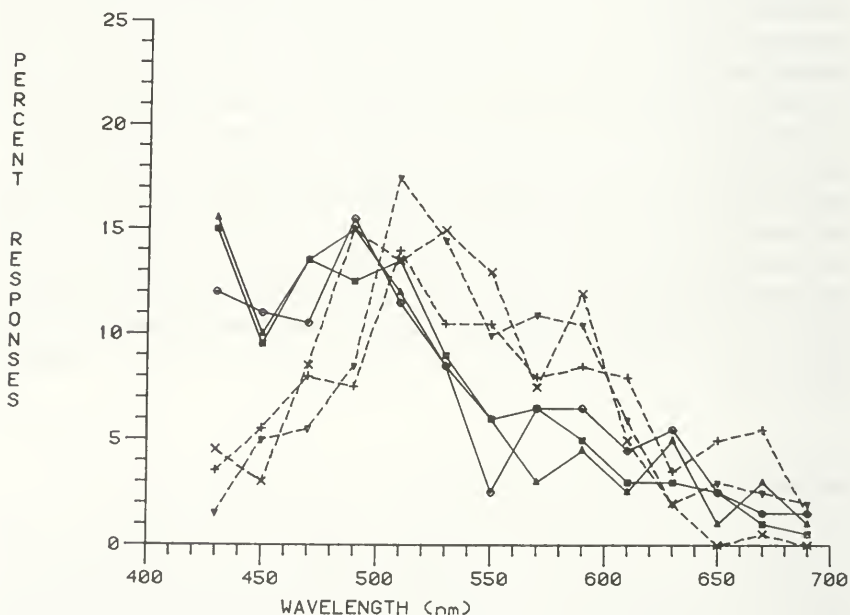


FIGURE 2. Generalization gradients after training to 490 nm (solid lines) and 510 nm (dashed lines) for six different fish from testing days 17-20.

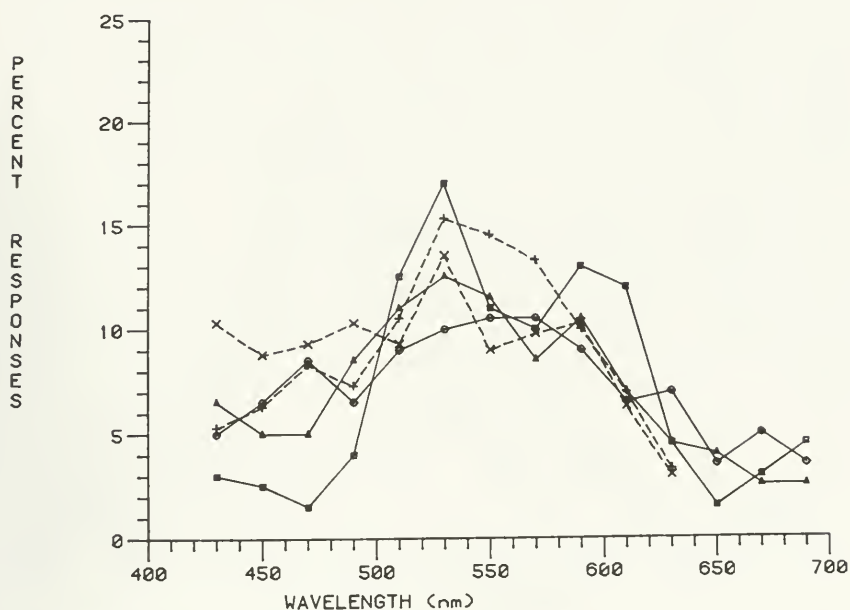


FIGURE 3. Generalization gradients after training to 530 nm from testing days 17-20 for five fish. The dashed gradients are from two fish for which 530 nm was the second training stimulus; the solid gradients are from three fish for which 530 nm was the first training stimulus.

testing session, the gradients peaked at the current training stimulus.

For consistency of comparison across the experimental conditions, the data from sessions 17-20 (or 18-21) for stimulus presentations without reinforcement will be presented. The animals first trained to 450 nm were given a single generalization session with a restricted range of wavelengths, to see how flat the initial gradient would be. Subsequent generalization sessions produced two day gradients, thus necessitating the use of days 18-21 for compatibility. Each two day gradient was computed by dividing the sum of the responses in the three unreinforced presentations of each wavelength by the total number of responses to stimuli without reinforcement on those days. The last two gradients, days 17/18 and 19/20, were then averaged and are presented in Figures 1-5. Figures 1, 2, and 5 each show individual generalization gradients for six different fish; Figure 4 shows gradients for the same three fish after training to one wavelength, obtaining a gradient, and retraining to a second.

The data from all three fish trained to respond to a 450 nm light transilluminating the Plexiglas disc and all three fish trained to a 490 nm light are presented in Figure 1. Although the functions peak

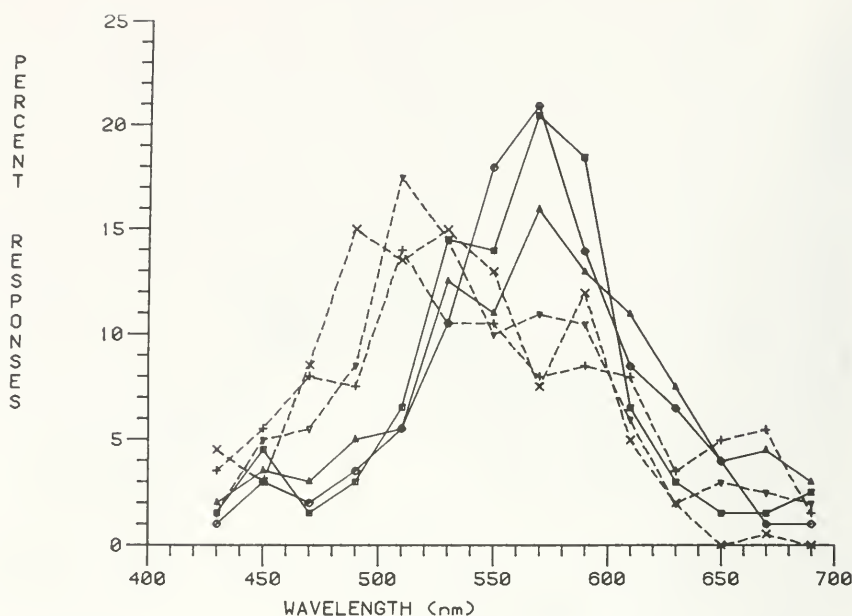


FIGURE 4. Generalization gradients after training to 510 nm (dashed lines) and 570 nm (solid lines) for the same three fish from testing days 17-20.

around their respective training stimuli, they have essentially the same shape; the animals respond to wavelengths lower than 490 nm. At wavelengths above 510 nm responding decreases and after 610 nm stays below five percent. This similarity occurs even though 490 nm was the third training stimulus after 530 nm and 590 nm for one group of fish, while 450 nm was the first training stimulus for the other fish.

Figure 2 shows the same three gradients to the 490 nm training stimulus together with gradients from all three fish trained to respond to a light of 510 nm. There is a clear separation of the 490 nm and 510 nm functions. At wavelengths below 470 nm responding by fish trained to 510 nm declines below five percent, while responding by the fish trained to 490 nm remains around 10-15 percent of total. Even the fish that generalized to 490 nm from the 510 nm training stimulus shows a steep decline in responses below 490 nm. The responding of the 490 nm animals declines to wavelengths above 510 nm, including one fish that generalized to 510 nm. The animals trained to 510 nm show generalization to all wavelengths between 530 and 590 nm. Two of these fish had secondary peaks around 570 and 590 nm, which could have been residual responding from previous 570 nm training.

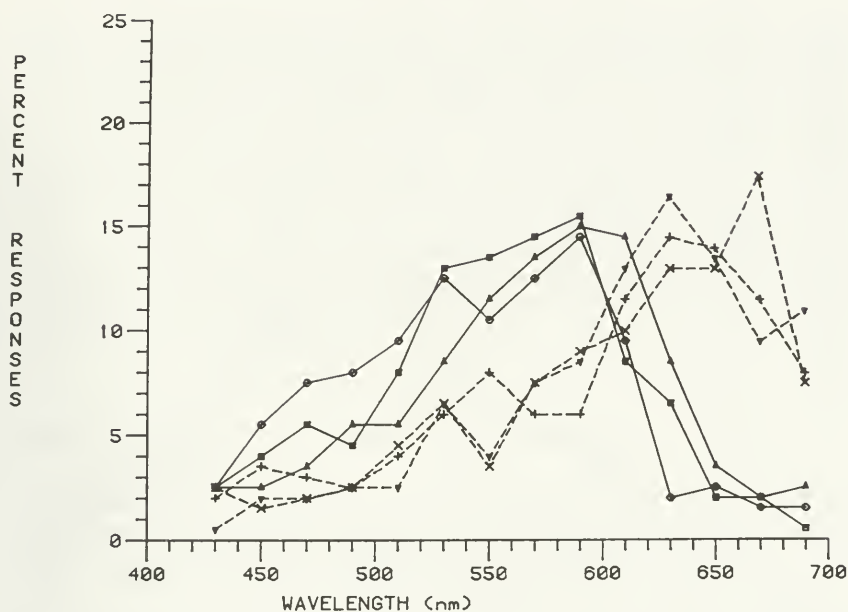


FIGURE 5. Generalization gradients after training to 590 nm (solid lines) and 630 nm (dashed lines) for six different fish from testing days 17-20.

Figure 3 shows the generalization gradients from all five fish trained to respond to a light of 530 nm. The two fish trained to 530 nm after 450 nm (dashed lines) seemed to show some residual responding below 490 nm and had some responding to all wavelengths lower than 630 nm, yielding a flat gradient; so a new group of three fish were given 530 nm as their initial training stimulus. Their three gradients (solid lines) also are rather broad and flat between 490 and 610 nm. Two of the new fish had responses above five percent between 430 and 490 nm. Two of the gradients display a secondary peak around 570 and 590 nm as did the gradients from the fish trained to 510 nm, even though those fish trained to 530 nm had not been reinforced at any other wavelength.

In contrast to the 530 nm gradients, the gradients from all three fish trained to respond to 570 nm are clearly peaked at the 570 nm stimulus. These are the solid lines in Figure 4, shown along with the gradients from the same fish to the 510 nm training stimulus (dashed lines) which were already presented in Figure 2. The 570 nm gradients have steep drops to below five percent responding for wavelengths both below 490 nm and above 650 nm. Both sets of gradients decline similarly on the long wavelength side, above 610 nm, while on the short wavelength side they are separated.

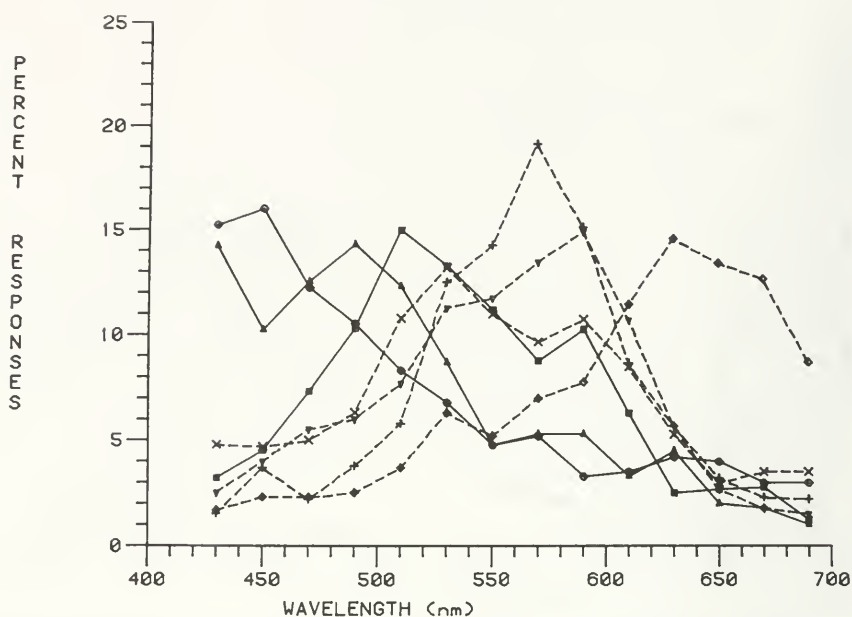


FIGURE 6. Generalization gradients from testing days 17-20 (18-21 for 450 nm) averaged from data for three animals. The gradients around 490, 530, and 590 nm are from the same three animals; a different group of three produced the 510 and 570 nm gradients; and the 630 nm gradient includes data from two fish from the 450 nm group.

Figure 5 shows the generalization gradients from all three fish trained to respond to 590 nm along with the gradients from all three different fish trained to a 630 nm light. The gradients around 590 nm are similar in shape to the 570 nm gradients although not as peaked. They have steep declines in responding to wavelengths above 590 nm (the training stimulus). The decline in responding to shorter wavelengths is very slight between 590 and 530 nm. The gradients to the 630 nm training stimulus are clearly different. Responding drops below ten percent at wavelengths of 590 nm and shorter, whereas there is more responding to wavelengths of 610 nm and above. All three gradients to 630 nm are alike even though 630 nm was the third training stimulus given to two of the fish and the only training stimulus for the third fish.

The data from the three fish trained at each wavelength were averaged and plotted on the same axes in Figure 6. As demonstrated in Figure 1, the gradients for the 450 and 490 nm training stimuli, on the left of Figure 6, show generalized responding to wavelengths below 490 nm and low levels of responding, below five percent, to wave-

lengths above 550 nm. On the right in Figure 6, the gradient to the 630 nm stimulus is different from any other gradient, with responding maintained to wavelengths longer than 610 nm, decreased responding to 590 nm and shorter wavelengths, and very little responding below 510 nm. The four middle curves show considerable overlap. All four have decreased responding between 590 and 630 nm. The curves for 510 and 530 nm have secondary peaks at 590 nm, while the curves for 570 and 590 nm have steeper declines below 530 nm than between 530 nm and the training stimuli. The largest separation is between the curves from the 510 and the 570 nm training stimuli as demonstrated in Figure 4.

DISCUSSION

The shape of the generalization gradients along the wavelength continuum indicates the way an organism groups wavelengths into color categories. There should be more generalization within a category, indicated by high peaks or flat slopes, and minimal generalization between categories, with steep slopes at the color boundaries. The question asked here is how many color categories do goldfish demonstrate. When the aforementioned rules are applied to Figure 6 there is clearly only one gradient for the long wavelengths above 610 nm. The peaks of the functions are all found at the training stimuli. Around 630 nm there is a gradual decline to 670 nm, and a steeper drop to 570 nm, with low responding to 510 nm and few responses at shorter wavelengths. Similarly, the gradients around 490 and 450 nm show generalization to 430 nm, steeper declines to 530 nm, and minimal responding above 590 nm. Figure 1 displays the closeness of the individual gradients to 450 and 490 nm, suggesting that they represent a single short wave function below 490 nm. These gradients also demonstrate the absence of generalization between the "blue" and "red" ends of the spectrum found in data from pigeons (Wright and Cumming, 1971) and humans (Boynton and Gordon, 1965). The lack of wraparound in the goldfish functions may be a result of the goldfish's sensitivity to ultraviolet, which extends the visible spectrum to short wavelengths below 400 nm (Hawryshyn and Beauchamp, 1985), where there is probably an additional color category.

The question remaining is whether the four middle wavelength functions represent one category or two broadly overlapping categories. All four curves have steep slopes above 590 nm, flatter slopes between 590 and 530 nm, and another steep drop below 530 or 510 nm. The close proximity of the long wavelength sides and the unexpected secondary peaks (without any previous training in the 530 and 570 nm groups) support a single category hypothesis. On the other

hand, the separation of the 510 and 570 nm functions on the short wavelength side, the distinctiveness of the 570-590 nm peaks from the 510-530 nm peaks, and the flatness of the 530 nm functions, support a dual category hypothesis. The flatness of the gradient around 530 nm was a surprise because flatness indicates a lot of generalization and 530 nm is the peak of one cone's spectral absorption function. The stimuli (450, 530, 630 nm) presented to the first group of fish were chosen to be close to the maximal absorption of the goldfish cones. The gradients to 530 nm, the second training stimulus, appeared to have so much residual responding to the shorter wavelengths around 450 nm that a new group of fish was given 530 nm as their initial training stimulus. As shown in Figure 3, although there was somewhat less responding to the shorter wavelengths, these three fish also gave very flat gradients. Therefore, some residual responding from previously trained stimuli did not alter the gradients' shapes dramatically. The flat gradients to 530 nm may thus indicate confusion between two color categories because it is near the cross-over point for two separate middle wavelength functions.

A comparison of these functions with the physiological data of Jacobson (1964) from the optic tectum supports the two category hypothesis. Tectal units, which were classified by Jacobson into three types: red-green, red-blue, and yellow-blue, had maxima in four spectral locations; 448-476 nm, 497-517 nm, 552-584 nm, and 605-651 nm. Jacobson emphasized that none of his units had a maximum response at 530 nm. These results support the four category hypothesis and fit well with the current functions around 450, 510, 570, and 630 nm. Neutral points were found by Jacobson between 497 and 517 nm, 517 and 552 nm, and 552 and 584 nm. The first neutral point is close to our crossovers between 490 and 525 nm, the second agrees with the hypothesized 530 nm crossing point, but the third is clearly different from the 595-608 nm crossovers from the current data. These 595-608 nm crossing points are closer to the transitions found by Beare (1973) in the ganglion cells, although she thought they represented "yellow" while our data clearly indicate that there is no color category at these wavelengths. Jacobson's neutral points between 552 and 584 nm from his "R-G" cells and a few of Beare's neutral points at 570 and 580 nm are more likely to be the "yellow" crossovers as the current data suggest a color category within this range.

Comparison with Yarczower and Bitterman's (1965) frequency gradients from their Experiment II yields some interesting similarities, in spite of the different methodologies. Their data are from testing days during which the stimuli, not matched for "brightness," were presented for 30 s with a 10 s inter-trial interval. The animals were reinforced for responses to the training stimulus before and after testing on each day. Yarczower and Bitterman's 580 nm curve has

a peak at 560 nm and a steep drop to 620 nm, similar to the 570 nm gradient of the present study; their 550 nm curve is broader than their 580 nm curve, as is our 530 nm curve. The almost symmetrical decrease in responses to 510 and 610 nm places the 550 nm gradient right in the middle of our middle wavelength group; but the departures from symmetry suggest that it is more similar to their 580 nm and our 570 nm functions because the decrease in responding to the shorter wavelengths is steeper than the decline in responding to longer wavelengths.

Yarczower and Bitterman compared their generalization gradients to a wavelength discrimination function to test the inverse hypothesis: the theory that areas of greatest generalization are those in which discrimination is the poorest and areas of least generalization should correspond to those wavelengths where discrimination is the best. Our data can be compared to a more recent wavelength discrimination function which covers the entire spectrum from 400 to 650 nm with the stimuli matched for "brightness" (Neumeyer, 1986). The area of good discrimination at 600-610 nm is right at our 595-610 crossover points and we also have some crossovers around 500 nm, the region of the best discrimination, thus supporting the inverse hypothesis. Given the range of crossing points in the present study, comparison of the goldfish gradients with those from pigeons and humans shows a remarkable correspondence of good discrimination and little generalization in the 595-605 nm region. This agreement occurs in spite of differences in the peaks in the cone spectra for these groups. Pigeons have a definite crossover at 540 nm; humans do not; goldfish show a tendency toward broad generalization in this spectral region. Both humans and goldfish have good discrimination and crossovers in the 490-500 nm region. Our study therefore extends comparison of behavioral wavelength categorization to show consistencies between the goldfish data and those from other animal groups. Perhaps, as Neumeyer (1986) suggests, the convergence of processes from diverse groups of animals relates to the daylight spectrum of the sun.

The present data were obtained with stimuli photopically equated based on data by Yager (1967) for the freely swimming fish. Other photopic sensitivity functions have been suggested in the literature (Beauchamp, 1978; Powers, 1978; Neumeyer, 1984). The variations in the shapes and peak sensitivities of these functions are related to differences in the task and adaptation conditions. Yager's data, obtained with freely moving fish, were chosen as the closest procedurally to our training conditions (Yager, 1970). Although the fish in the present study were in the dark between stimulus presentations, the stimuli were presented above photopic threshold. This 15 s dark interval was needed for the experimenter to change stimulus conditions and is not sufficient for dark adaptation to occur. The sim-

ilarity of our data to Yarczower and Bitterman's may reflect the robustness of the wavelength generalization procedure in spite of intensity differences.

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DOMINANCE BEHAVIOR IN ASEXUAL GECKO, *LEPIDODACTYLUS LUGUBRIS*, AND ITS POSSIBLE RELATIONSHIP TO CALCIUM

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ABSTRACT: Investigations of dominance behavior and its relationship to calcium gland size were conducted in the asexual gecko, *Lepidodactylus lugubris*. In an initial study, geckos, immediately after laying eggs, were randomly assigned to one of six groups where time of social contact (2 vs. 7 days) and type of social contact (direct experience with a gravid or non-gravid gecko or indirect experience) were varied in a 2×3 factorial design. Behaviors displayed by geckos in social contact were systematically recorded. Dominance hierarchies were readily formed between gecko dyads that received 7 days of social contact with each other. Dominance was not related to gecko size or reproductive state. A second study examined the relationship between dominance, calcium gland size and egg development. Geckos were housed in groups of 4 for 28 days and were subsequently transferred into either dyads or housed individually for an additional 28 days. During the final 28 days, half of the geckos received extra calcium. Dominance, size of calcium glands and egg development were recorded. Dominant geckos developed a greater number of eggs and had larger initial calcium glands than subordinates, but extra calcium was not related to gland size. The function of dominance in *L. lugubris* populations may be two-fold: it may act as a spacing mechanism in low density environments and may facilitate the development and laying of eggs by more nutritionally fit individuals in high density environments.

Dominance hierarchies are well documented in a variety of sexual vertebrate species and are usually associated with aggression and lowered reproductive success of subordinates (i.e. primates, Abbot, 1987; birds, Ekman, 1987; wolves, Packard et al., 1985). The data on dominance and its relationship to aggression and reproductive success are more equivocal in asexual vertebrates. Leuck (1985) found that individuals of the parthenogenic species, *Cnemidophorus uniparens*, were less aggressive than sexual *Cnemidophorus* species and seldom engaged in biting or chasing. The asexual whiptails were also reported to form weaker dominance relationships than sexual whiptails. In contrast to Leuck's research, however, Grassman and Crews

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(1987) found that asexual *C. uniparens* readily formed dominance hierarchies.

Bustard (1970) found that female geckos of sexual species occasionally regulated their numbers through aggression, however, Frankenberg (1982) reported little aggressive behavior in the parthenogenic gecko, *Hemidactylus garnotti*. When one *H. garnotti* approached another, the stationary gecko usually attacked and the approaching gecko always retreated. *H. garnotti* did not form stable dominance hierarchies or establish territories even though they preferred certain locations in their enclosures. Again, in contrast, Brown and Sakai (1988) found that the mourning gecko, *Lepidodactylus lugubris*, formed dominance hierarchies and that egg development was related to dominance. Dominance behavior was also related to egg production in *C. uniparens* (Grassman & Crews, 1987; Gustafson & Crews, 1981).

Geckos are unusual among reptiles because they lay calcareous shelled rather than parchment shelled eggs (Bustard, 1968). Calcium glands are visible in most adult geckos' necks (Ruth, 1918) and change size relative to the female's reproductive state (Ineich & Gardner, 1989). The reduced fecundity of subordinates may be related to stress and its effects on calcium. Stress is related to decreased calcium levels in some species (i.e., chickens, Odom, Harrison, and Botte, 1986; rats and mice, Watanabe, Ho, and Haskins, 1987) or altered and inefficient calcium storage as in porcine stress syndrome (Basrur, Frombach, and McDonell, 1983; Cheah & Cheah, 1979). Lowered calcium levels are also associated with increased mortality and abnormal eggs in chickens (Brugh & Beard, 1986). Therefore, a proximate cause of the decreased fecundity observed in subordinate mourning geckos may be decreased levels of available calcium.

The two present studies were designed to extend our knowledge of the variables important in egg development in *L. lugubris*. The first study examined the formation of dominance hierarchies in *L. lugubris*. The second study examined calcium gland size and its relationship to dominance and egg development in *L. lugubris*.

METHODS

General Housing Conditions

The geckos were provided with water, food (meal worms, grasshoppers, and fruit flies) and a vitamin (Brand name Vionate)/corn syrup mixture ad libitum. To provide a humid and moist environment, the enclosures were misted with water each morning. Each enclosure floor was covered with approximately 2 cm of pebbles to per-

mit digging. Sphagnum moss was placed on the pebbles to provide the geckos with hiding places and to maintain the moisture within the enclosure. One platform, constructed of two pieces of wood so that a crack was formed, was placed in each enclosure. The platform was designed to mimic the geckos' daytime hiding places. A 12 hr light/dark cycle was maintained with lights turned on at 6.00 and off at 18.00 hr. Additional external fluorescent lights were placed near each enclosure providing the geckos with heat, and were turned on at 8.00 and off at 12.00 hr. The laboratory room was open to the natural tropical environment of Hawaii Island through windows along one wall; lab temperatures varied from 72 to 78°F.

STUDY 1

Procedure

Study 1 was designed to document how dominance hierarchies are formed in *L. lugubris* and whether dominance is related to the gecko's reproductive state. Sixty *L. lugubris* were collected on 21 and 22 January 1987 between 19.00 and 21.00 hr at the University of Hawaii, Hilo. The study began 21 January 1987 and continued until 10 August 1987 when the last gecko laid its eggs. Geckos were initially housed in aquaria (51 cm \times 28 cm \times 31 cm) and checked weekly for egg development. Eggs greater than 1 mm in diameter were observed by placing the animals in narrow plexiglass boxes and examining their translucent ventral surfaces. When egg development was first noticed, the geckos were removed from the communal enclosures and randomly assigned to single plexiglass enclosures (32 cm \times 18 cm \times 23 cm). Geckos that did not lay at least one egg were not used as subjects; therefore all experimental geckos were synchronized in terms of their reproductive cycles. The first 36 geckos (experimental geckos) to lay eggs were randomly assigned to one of six groups ($n = 6$) which comprised a 3 \times 2 (condition \times days) factorial design. Geckos were placed with 3 types of stimulus gecko (stimulus geckos were obtained from our lab collection): a gecko with no visible sign of egg development (non-gravid condition), a gecko with visible eggs (gravid condition), or in a divided enclosure in which the gecko was able to see and hear another non-gravid gecko but could not touch it (audio/visual condition). Geckos remained in the social situation for either two or seven days.

Eight 15 min event recordings were obtained each day for geckos that were housed with a stimulus gecko with which they could physically interact (2 and 7-days—gravid conditions; 2 and 7-days—non-gravid conditions) each hour between 6.00 and 10.00 hr and again

TABLE 1
Interactive Behaviors Observed Between Geckos with Descriptions

<i>Behaviors</i>	<i>Descriptions</i>
In proximity	Less than 3 inches apart, from 2 to 15 min.
Orient to	Gecko turns head toward another
Face to	Gecko turns body toward another
Approach	Gecko moves toward another, including mutual approaches and chases, but excluding lunges
Click	Rapid, sharp sound
Rurr	Extended, low guttural sound
Push-up	Gecko moves upper body up and down
Lunge	Gecko plunges toward another
Bite	Gecko mouths the other usually on the neck or tail
Touch	Physical contact excluding biting
Displacement	Gecko occupies the position of another after the second moves away
Orient away	Gecko turns head away from another
Face away	Gecko turns body away from another
Back-up	Gecko moves away from another using a backward motion
Move away	Gecko moves away from another in a forward motion

between 17.00 and 21.00 hr. Therefore, geckos in the 2-day condition were observed for 4 hr, while those in the 7-day condition were observed for 14 hr. The behaviors classified as interactive are summarized in Table 1. Dominant geckos were defined as geckos that did not flee as often as their cagemates in encounters where one gecko clearly fled from another. Stable dominance hierarchies were defined as those in which one gecko was consistently dominant to the other during the last half of the observations (i.e., the last 24 hrs in the 2-day condition and the last 3 ½ days in the 7-day condition). The positions of the geckos relative to one another were also systematically recorded for geckos in the audio/visual condition.

Results

Interactions between gecko dyads were highest during the first 24 hr after they were placed together, and most interactive behaviors significantly decreased during the second 24 hr (Table 2). Both experimental and stimulus geckos exhibited similar decreases in orienting

TABLE 2
Behavioral Differences Observed in Geckos Across the First
vs. the Second 24 hr They Were Placed Together.

	0-24 hrs		25-48 hrs			
Behavior	MN	SE	MN	SE	$F_{(1,22)}$	p
<i>Experimental Gecko</i>						
Orient/face to	.4	(.3)	.2	(.2)	9.2	.006
Approach	.5	(.4)	.2	(.3)	9.3	.006
Click	3.0	(1.9)	.9	(1.3)	2.8	.11
Bite/lunge	.1	(.1)	.0	(.1)	3.8	.06
Orient/face away	.2	(.1)	.1	(.1)	6.1	.02
Move away	.3	(.4)	.1	(.3)	5.6	.03
<i>Stimulus Gecko</i>						
Orient/face to	.4	(.3)	.1	(.2)	10.6	.004
Approach	.5	(.4)	.1	(.2)	11.3	.003
Click	1.9	(2.4)	.8	(1.8)	3.2	.09
Bite/lunge	.1	(.1)	.0	(.1)	4.2	.05
Orient/face away	.2	(.2)	.1	(.1)	2.9	.10
Move away	.4	(.2)	.1	(.2)	13.8	.001

or facing to, approaching, clicking at, lunging and/or biting, orienting or facing away from, and moving away from the other gecko. In the 2-day groups, only 6 of the 12 dyads formed stable dominance hierarchies. In contrast, in the 7-day groups, stable dominance hierarchies were formed in 11 of the 12 dyads (the one exception was in the 7-day gravid condition). In the 7-day gravid condition, the gravid gecko was dominant 3 times and the experimental (non-gravid) gecko 2 times. Therefore, being gravid did not necessarily give the gecko an advantage in dominance contests. In both 7-day groups the dominant gecko was larger than the subordinate in 45% of the dyads, equal in size in 18%, and smaller than the subordinate in 36% of the dyads (Overall $\bar{X}(\text{DOM}) = 43$ mm, $s(\text{DOM}) = 1.5$ mm; Overall $\bar{X}(\text{SUB}) = 42$ mm, $s(\text{SUB}) = 2.7$ mm). In all stable dominance hierarchies (17/17) the dominant gecko controlled the platform by the end of the observations.

All geckos displayed behaviors associated with dominance behavior. Interactions between gecko pairs in the 7-day conditions were analyzed in detail. Dominant geckos were more likely to initiate and end encounters by clicking than subordinates; this difference was statistically significant using the Sign test ($T = 0$, $N = 11$; $p < .01$). Subordinate geckos usually initiated encounters by simply orienting

to or facing the dominant gecko without subsequently approaching; a behavior seldom observed in the dominant geckos. This difference was statistically significant using the Sign test ($T = 0$; $N = 6$; $p < .05$).

Whether the geckos were in the gravid condition influenced their reactions to another gecko. Geckos in the gravid condition many times displayed no visible reaction after their cagemates initiated an encounter (18/47 encounters). Geckos in the non-gravid condition, however, seldom reacted to an encounter by "not responding" (5/73 encounters). This difference was found to be statistically significant using the Mann-Whitney U ($U = 27$; $n = 5$ & 6 ; $p < .05$).

Geckos in the audio/visual conditions, although not able to physically interact, oriented themselves so that they could view each other in 36% of the observations. Five of the six geckos in the 7-day audio/visual condition were observed mutually clicking at each other at least 2 times during observations; this differed from clicking observed in the gravid and non-gravid conditions when only one gecko clicked at a time.

STUDY 2

Procedure

Study 2 was designed to see if calcium gland size was related to dominance in *L. lugubris*. Thirty-two *L. lugubris* were collected on 31 January ($n = 16$) and 14 February 1989 ($n = 16$) at the University of Hawaii, Hilo. Only geckos that showed no visible eggs were collected. Two replicates of the study were conducted. In both replicates 16 geckos were randomly assigned to one of four communal enclosures ($n = 4$) after their snout-vent lengths and calcium glands were measured, and after they were paint marked with non-toxic tempera paint. Two observers, blind to the geckos' dominance status, independently measured the calcium glands (inter-observer reliabilities ranged from + .5 to + .84 with a mean of + .72).

Geckos were kept in the communal enclosures for 28 days. Fifteen minute event recordings were obtained on each enclosure in a random sequence between 8.00 and 9.00 hr five days a week (total observation time per enclosure = 5 hr). Observations were done in order to determine the dominance rank of each gecko. Dominance was defined by the number of times a gecko ended an interaction with the other gecko moving away and by the ability of a gecko to maintain control of the platform over other geckos in the enclosure (See results obtained in Experiment 1 above).

After 28 days in the communal enclosures, calcium glands were

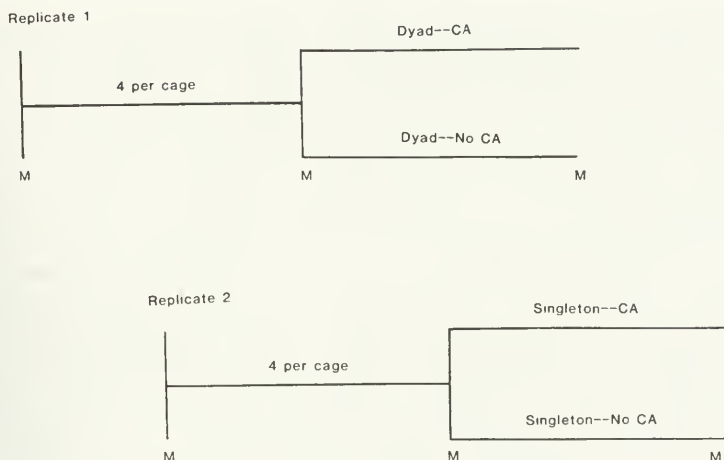


FIGURE 1. Experimental design for experiment 2. M indicates when a measurement of the geckos' calcium glands was obtained, CA indicates groups that received extra calcium in the form of gecko egg shells, and horizontal lines represent 28 day periods.

remeasured (See Figure 1). The geckos in Replicate 1 were divided into dyads and transferred to smaller plexiglass enclosures. The most dominant and most subordinate geckos were housed together and the intermediately ranked geckos were housed together. One gecko in Replicate 1 escaped during the first 28 days. Only the most dominant and subordinate animals were kept from this cage; the remaining gecko was released ($n = 14$). Calcium supplements which consisted of gecko egg shells were supplied to 3 of the 7 dyads (2 cages containing dominant/subordinate geckos and 1 with intermediate geckos). For the next 28 days, the geckos' positions in the enclosure were noted each morning with special attention to which gecko controlled the platform.

In Replicate 2 after the communal experience, the geckos were housed alone for 28 days. This was done to observe how a less stressful environment in terms of dominance would affect the size of their calcium glands. Geckos were checked weekly for egg development and enclosures daily for oviposition. Calcium glands for both replicates were measured 28 days after the geckos were transferred from communal cages (See Figure 1). All geckos at the end of the study were released near their capture sites.

Results

At the end of 4 weeks, 13 out of the 15 dominant geckos had developed eggs whereas only 4 out of the 15 subordinates had devel-

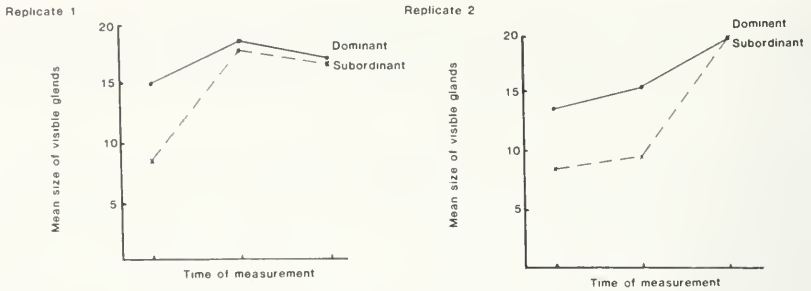


FIGURE 2. Summary of the calcium gland measurements for both Replicate 1 and Replicate 2. The first measurement was made the morning after the geckos were captured, the second measurement 28 days later after the geckos had been housed as quadruplets, and the third measurement 28 days later after geckos had been housed as either dyads (Replicate 1) or alone (Replicate 2).

oped eggs. The difference in egg development between dominant and subordinate geckos was significant ($\chi^2_{(1)} = 11.0$; $p = .01$; data from both replicates are included). Subordinates in both replicates had significantly smaller initial calcium glands than the dominants ($F(1,28) = 6.2$; $p < .05$; Figure 2). In Replicate 1, the subordinates' calcium glands increased up to week 4 whereas the size of the dominants' calcium glands remained relatively stable for the entire 8 weeks (Trials effect was significant; $F(2,24) = 7.2$; $p < .006$ using Greenhouse Geisser probability). On the other hand, in Replicate 2 the subordinates' calcium glands remained smaller than the dominants' through week 4 of the study and then increased in size after the geckos were housed alone (Trials effect was significant; $F(2,28) = 12.1$; $p < .0005$ using Greenhouse Geisser probability). The extra calcium some groups received in the form of gecko egg shells did not affect the size of geckos' calcium glands.

There were 13 geckos from both replicates with no eggs at the end of week 4, seven of these subsequently received extra calcium and six did not. Five of the seven that received calcium supplements developed eggs whereas only one of the six that did not receive calcium supplements developed eggs. Therefore there was a tendency for geckos that received calcium supplements to develop eggs over those which did not receive extra calcium.

DISCUSSION

All gecko dyads and quadruplets in the present studies attempted to establish dominance hierarchies; hierarchies stabilized by day 7

and half (6/12) by the end of 2 days. Dominance was unrelated to the reproductive state of the gecko. The behaviors displayed by both dominant and subordinate geckos were stereotypic with dominants much more likely to vocalize than subordinates. Unlike the parthenogenic gecko, *H. garnotti*, which defended a relatively small moveable area surrounding its body (i.e. its personal space, Frankenberg, 1982), *L. lugubris* dyads established stable dominance relationships, and the dominant gecko gained a resource, the small platform. Geckos are crack dwelling animals (Jones et al., 1978), and because the platform provided the only "crack" in the enclosure, dominant geckos obtained the best hiding place.

Dominant animals in Study 2 developed more eggs than subordinates. Brown and Sakai (1988) also found that dominant *L. lugubris* developed more clutches of eggs than subordinates, and dominant *C. uniparens* were found to be more fecund than subordinates (Grassman & Crews, 1987; Gustafson & Crews, 1981). Dominance may work as a spacing mechanism in geckos. For example, if a particular gecko is subordinate, it may be advantageous for it to move to a different place where there are either no geckos or where it can dominate. On the other hand, when geckos become numerous, as they are in many areas on the island of Hawaii, the most fit animals (i.e. dominants) may be the ones laying the majority of the eggs.

Because geckos lay calcareous shelled eggs (Bustard, 1968), animals with higher levels of calcium could be considered more fit than those with lower levels. We found that subordinate geckos in our quadruplets (Study 2) had initially smaller calcium glands than dominants, and that the calcium glands of subordinates increased in size when they were removed from social situations. Additionally, geckos that had not previously shown signs of egg development began to develop eggs when they received supplemental calcium. A proximate cause of decreased egg development in subordinate *L. lugubris* may therefore be decreased levels of calcium for egg shell formation.

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BOXING IN RED KANGAROOS, *MACROPUS RUFUS*: AGGRESSION OR PLAY?

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ABSTRACT: Fighting in a boxing style is the most spectacular behaviour of red kangaroos, *Macropus rufus*, yet its structure and function have not been analysed in detail. Patterns of sparring, kicking and wrestling occur between mothers and young (especially males), in formalized contests between males, and in escalated conflicts over resources (shelter, water, oestrous females). Observations were made of fighting behaviour in free-living and captive individuals. The frequency of fighting between various age/sex classes in the field was determined and the structure of fighting over a water resource was analysed from a 12 h videotape record. These results were compared with an analysis of 85 videotaped plus 35 other fights observed in a captive group of eight males (age 1 - 7 year). These fights were formalized contests which did not involve or resolve any immediate conflict over a resource. Such fights share many of the properties ascribed to play-fighting. They are initiated with invitational behaviour that does not include characteristic threat behaviour seen in fights over a resource. They involve self-handicapping, some lack of dominance distinctions, and usually several bouts occur interrupted by mutual pauses. The structure of the fight suggests that the main goal is to push or wrestle the opponent off balance and down to the ground rather than inflict potentially injurious kicks as seen in resource conflicts. Furthermore larger opponents often adopt an inferior flat-footed stance and dominants and/or winners kick significantly less than losers. The context, goals and structure of these non-resource based fights suggest that they are a form of play-fighting. Selection of play partners on the basis of size/dominance or kinship indicate that such play-fighting in red kangaroos is neither truly cooperative nor disruptive and selfish. The behaviour most likely functions as a form of non-damaging assessment of opponents with benefits in skill development in younger individuals.

The red kangaroo *Macropus rufus* is a large grazing macropodid from the inland plains of the Australian arid zone. Males may attain body weights of 90 kg or more but females rarely exceed 35 kg. The mating system is one of hierarchical promiscuity (after Wittenberger, 1979), male competition for mates is intense and usually the largest male gains an exclusive consort relationship with an oestrous female (Croft, 1981). Popular mythology of kangaroo behaviour (e.g. Williamson, 1978) would have it that a rival's disembowelment and death is a frequent consequence of male fights. However, death as a

result of fighting has only been documented in captivity (Sharman & Calaby, 1964). As in other animal species, fatal wounding is by no means a common result of such fights.

In red kangaroos, fighting occurs in two main contexts: (1) conflict between two or more individuals in disputed access to a resource, whether a shelter site, water or (for males) an oestrous female; and (2) circumstances where no resource is in immediate dispute (Croft, 1981). Resource-related and resource-unrelated fighting may indicate behaviour in red kangaroos that is analogous to 'serious' and 'play-fighting' (Fagen, 1981; Hole & Einon, 1984), respectively, in other mammal species. Play is a common phenomenon in endothermic vertebrates (Fagen, 1981) and play-fighting is typical of sexually dimorphic species (Symons, 1978). However, a satisfactory definition of play has proved vexing (Martin, 1984) and it is usually identified as behaviour which lacks an obvious goal and is therefore not immediately concerned with the participants' current survival, occurs in specific contexts, and may include unique play signals (Hole & Einon, 1984). Play and non-play are usually distinguished from their structure (Henry & Herrero, 1984; Owens, 1975; Bekoff, 1978) and so an operational definition of play is often employed.

Behaviour such as play-fighting may use motor patterns that mimic those used in competitive fighting for a limited resource. This makes the discrimination of serious fighting from play-fighting difficult. However, play patterns may be incomplete, inhibited, exaggerated or uneconomical, repetitive, sequentially unordered or re-ordered, causally distinct and even unique to the play context (Fagen, 1981). Pellis and Pellis (1987) argue that only the last of these criteria unambiguously distinguishes play and that few, if any, studies have successfully defined play by the other structural criteria listed. Pellis (1988) promotes an analysis of the targets attacked and defended in play-fighting and serious fighting as an objective measure of the differences between the two behaviour categories. Apart from potential differences in structure, the selection of partners may differ between play and non-play contexts. For example, smaller individuals may actively avoid agonistic interactions with larger ones but engage them in play-fighting since play may serve one or more of several functions—motor or cognitive training (Bekoff & Byers, 1981), regulation of developmental rates (Fagen, 1981) and socialisation (Poirier & Smith, 1974)—where interaction with a larger individual is of benefit. However, like the defining characteristics of play, functional hypotheses about this behaviour are contentious (Martin, 1984; Hole, 1988).

This study examines the structure of fighting behaviour in red kangaroos in both resource-related and resource-unrelated contexts to determine if the behaviour performed when resources are not in con-

study. Each yard had a shelter, a self-filling water trough, and a food shed which supplied *ad libitum* pelleted food supplements. Neither food, water, or shelter was limiting.

Procedure

Two categories of fighting behaviour were distinguished based on their context: resource-related (RR) and resource-unrelated (RU) fighting. Results on rates and durations of RU fighting in various age/sex classes of free-ranging kangaroos were derived from unpublished data collected on the social behaviour of red kangaroos. This study is described in Croft (1981). The data set comprised 1500 h of focal-animal sampling of the various age/sex classes during the diurnal period.

Results on RR fighting behaviour resulting from competition for a water resource were derived from unpublished data collected during a study described in Croft (1985). A 12 h videotape record of agonistic behaviour between red kangaroos at a water trough in mid-summer was used. This record was collected from 2000 - 2400 h using a Sony Portapak VCR and Sony camera attached to a Javelin night vision device. Observations were made from a hide located 35 m from the trough and the trough was illuminated with dim red light.

For the captive study, observations were made from a small, elevated hide set up along one of the fences in a position that offered an unobstructed view of all animals. Observations, totalling 100 h, were made twice weekly for periods of 3 h around dusk and the following dawn of two consecutive days for six months (March - August). Night-time observations were made under red-filtered lights. All male-male fights (and 'fights' involving females, usually mother-young interactions) were recorded using a Sony Portapak VCR and camera. A more complete record of each male's social behaviour was obtained by focal sampling each male for a half-hour period, recording all its social interactions on audiotape. The order of these focal watches was rotated so that each male was observed over the range of different times within observation periods. Interactions were defined as being non-agonistic, agonistic, or sexual after Croft (1981). The initiator of each interaction was noted and, for agonistic interactions, the 'winner' or 'loser' identified. The outcome of agonistic interactions where one individual supplanted another (i.e., exclusive of fights) was used to define a male dominance hierarchy using the methods of Russell (1970).

The incidence of RR fights in the captive group was rare ($< 1\%$ fights) and so further analysis was confined to RU fights. The videotapes of RU fights were analysed in slow motion (0.22 of real time). Every action of the combatants was recorded in the sequence it occurred on a Datamyte 904 event recorder allowing resolution of be-

TABLE 1
Frequency of Fights and Mean and Range of Fighting Bouts
between Various Size/Sex Classes of Red Kangaroos in the
Field

<i>Dyad</i>	<i>Frequency per 100h</i> (<i>n</i>)	<i>Mean bouts per fight</i> (<i>range</i>)
<i>Male large - Male large</i>	3.5 (3)	1.3 (1-2)
<i>Male large - Male medium</i>	2.6 (5)	2.8 (1-6)
<i>Male medium - Male medium</i>	5.1 (30)	5.1 (1-16)
<i>Female - Female</i>	0.3 (2)	1.0 (1-1)
<i>Male young - Mother</i>	9.0 (8)	1.6 (1-4)
<i>Female young - Mother</i>	4.8 (4)	1.3 (1-4)

havioural durations to 0.01 min. The Datamyte record was transmitted to an Apple II computer for further analysis of the frequency, duration, and transition frequency of each behaviour. The following behaviour units were used (see also Croft, 1981): approach (> 1 m to < 1 m), mutual nose sniffing, sniffing another body part of opponent, face (head oriented towards opponent), face away (head oriented away from opponent), stiff-legged walk (individual walks slowly on tips of toes with back arched accentuating body size), upright stance (standing flat-footed with back vertical), high standing (standing on tips of toes and tail, fully extended vertically), forearms locked (both forearms out-stretched and holding opponent's arms), head arch (head tilted back, nose upwards, throat exposed to opponent), pawing (raking body surface of opponent with both forepaws), hit (striking opponent with one forepaw), push (forcing opponent backwards), push down (forcing opponent towards the ground), push away (forcing opponent to disengage), kick (striking opponent with both hindfeet while balanced on tail), allogrooming, selfgrooming (with body part groomed/scratched), mouthing (nibbling head region of opponent), licking forearms, pause (both individuals standing apart on forepaws and hindfeet), move away slowly (walk), move away rapidly (hop), simultaneous withdrawal, chase, and feed.

In both field and captive studies, a fight was defined as any interaction involving one or more of the units forearms locked, pawing, hit, kick and the three pushing actions. RU fights typically extended over two or more bouts; i.e., sequences involving one or more of the

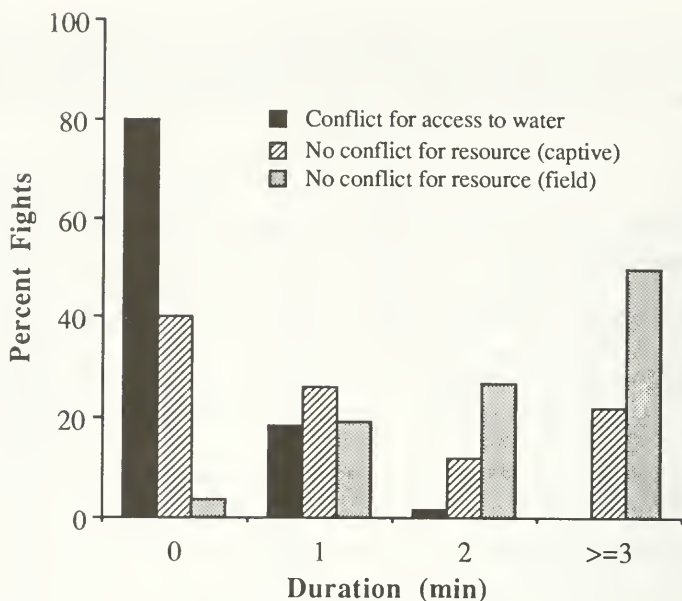


FIGURE 2. Comparison of the durations of RR fights over access to a resource (water) in the field, and RU fights where no access to a resource is disputed in the field and captivity.

above units were interrupted by pauses in which participants remained in physical contact or within close proximity (< 2 m), usually standing or grooming. Thus, the duration of a fight was determined from the time of initial contact between the participants to the time of withdrawal of one or both to distances > 2 m. A bout was distinguished as a period in which one or both participants performed one or more of the characteristic fighting behaviours.

RESULTS

Structure of Fights

In the field, RU fights occurred between all age/sex classes except adult male-female dyads (Table 1). Fights were least frequent between females and most frequent between mothers and their male young-at-foot. Among males, fights were most common between medium-sized (20 - 60 kg) males; i.e., males which were sexually mature but inferior in competition for mates (Croft, 1981). Fights typically occurred over one or more bouts. Medium-sized males engaged in longer fights with multiple bouts relative to other dyads (Table 1).

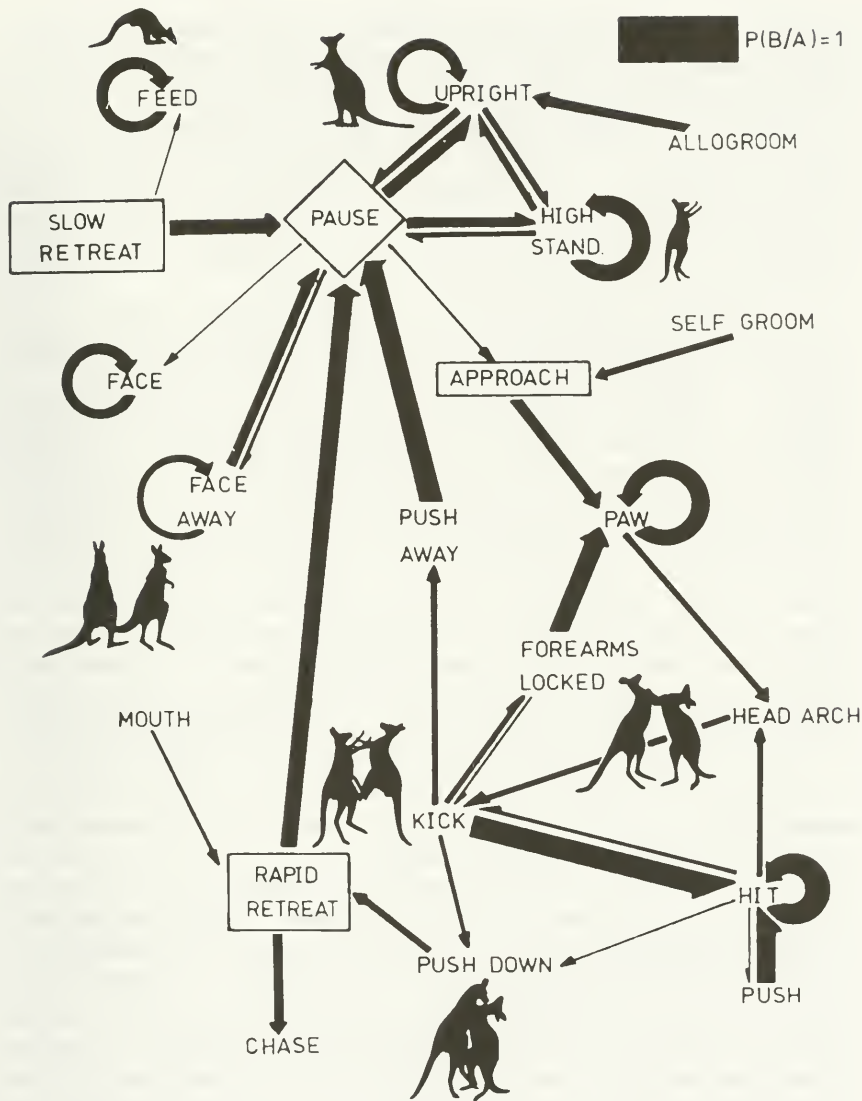


FIGURE 3. Significant positive transitions for inter-individual fight sequence derived from pooled data for 85 videotaped fights in captive group. Thickness of arrow indicates transition probability ($P[B/A]$).

To determine if structural differences occurred between fights involving a conflict over a resource (RR fights) and those not immediately resource-based (RU fights), RR fights at water in the field and RU fights in the captive group were analysed. Data on the duration of RU fights in the field were also used. There were clear differences.

RR fights at water were significantly shorter than those not involving resource competition (Figure 2), i.e., RU fights in either captive or field populations. Significantly more RR fights at water (76%, $n = 25$) were preceded by threat behaviour (i.e., stiff-legged walk, biting at sternum or full vertical body extension) than RU fights in the captive group (6%, $n = 85$) (Fisher Exact test, $p < .001$). In RR fights at water, the winner was significantly more likely to kick its opponent (83%, $n = 18$) than in RU fights in the captive group (19%, $n = 62$) ($X^2 = 18.03$, $p < .01$).

A number of other structural features of the RU fights in the captive group suggested that they were more analogous to play-fighting than to competitive fighting. A composite picture of the fight sequence was determined by combining the inter-individual behaviour sequence determined from the 85 RU fights recorded in the captive group (Figure 3). The core fighting behaviours are shown in the bottom right. The goal of the fight appears to be gaining a superior position to 'push down' the opponent leading to its rapid retreat. The most potent weapon of the kangaroo, the kick delivered with the full force of the hopping muscles, is not directly related to defeating an opponent. In fact, kicking may be employed as a retaliatory behaviour against the pushing thrusts of an opponent. Winners of fights push, push away, and push down significantly more frequently than losers, whereas the latter paw and kick significantly more frequently (Table 2). Losers were also significantly more likely to deliver the first (42/49 fights, Binomial test, $p < .001$) and last kick (41/49 fights, Binomial test, $p < .001$) in a fight. Thus, winners were not reserving a kick as a 'king hit' to terminate a fight.

The dominance relationships between the eight captive males were determined from success in supplanting interactions. The males were ranked in descending order as follows from the proportion of aggressive interactions (excluding fights) won (shown in parentheses): M1 (0.94), M2 (0.74), M3 (0.66), M4 (0.51), M5 (0.49), M6 (0.39), M7 (0.27), and M8 (0.21). In fights where kicking occurred, it was the subordinate (48 fights) that was significantly more likely to kick than the dominant (9 fights) (Binomial test, $p < .001$). Thus, the dominant individual appeared to be restraining its kicking behaviour while interacting with a subordinate in these RU fights which was not the case for at least the winners of RR fights as shown above. This form of possible 'self-handicapping' was further indicated by the stance adopted by larger individuals while fighting with smaller ones in RU fights. A measure of the percent difference in the time spent in an upright or highstanding posture for dominant and subordinate was calculated from percent difference = $100 \times (D_d - D_s) / (D_d + D_s)$ where D_d = time dominant spends in posture and D_s = time subordinate spends in posture. If individuals were of the same size class then the

TABLE 2
Comparison of the Mean (\pm SE) Frequency per min of
Behaviour shown by Winners and Losers in Videotaped Fights
($n = 80$) among Captive Males

<i>Behaviour</i>	<i>Winner</i>	<i>Loser</i>	<i>Z*</i>	<i>P</i>
Winner > Loser:				
<i>Approach</i>	0.63 \pm 0.10	0.61 \pm 0.24	2.48	< .05
<i>Selfgroom</i>	0.67 \pm 0.14	0.32 \pm 0.11	3.30	< .001
<i>Face</i>	0.22 \pm 0.06	0.10 \pm 0.03	2.75	< 0.01
<i>Upright</i>	1.55 \pm 0.19	1.25 \pm 0.21	2.50	< .05
<i>Hit</i>	7.82 \pm 0.63	6.87 \pm 0.65	2.22	< .05
<i>Forearm Lock</i>	1.13 \pm 0.14	0.43 \pm 0.15	4.15	< .001
<i>Head Arch</i>	1.87 \pm 0.24	0.98 \pm 0.15	3.38	< .001
<i>Push</i>	0.63 \pm 0.11	0.24 \pm 0.11	3.27	< 0.01
<i>Push Away</i>	0.67 \pm 0.17	0.31 \pm 0.17	3.67	< .001
<i>Push Down</i>	1.84 \pm 0.24	0.59 \pm 0.18	4.83	< .001
<i>Feed</i>	0.62 \pm 0.13	0.46 \pm 0.12	2.16	< .05
Loser > Winner:				
<i>Paw</i>	3.65 \pm 0.46	4.94 \pm 0.40	3.12	< .001
<i>Kick</i>	0.42 \pm 0.20	1.64 \pm 0.25	4.24	< .001
<i>Slow Retreat</i>	0.11 \pm 0.05	1.12 \pm 0.22	4.97	< .001
<i>Fast-Retreat</i>	0.10 \pm 0.04	0.90 \pm 0.19	4.22	< .001

*Wilcoxon Matched-Pairs Signed-Ranks test and associated 2-tailed probability

difference between dominant and subordinate was negligible (Figure 4). However, if the opponents were of different size classes then the dominant spent more time in the upright posture and the subordinate in the highstanding posture thus bringing them to equivalent sizes.

Another feature of play-fights is that role reversals, either dominant/subordinate or attacker/defender, may occur (Hole, 1988). This structural feature for RU fights was examined from the perspective of reversals in dominant/subordinate roles. However, success in RU fights followed the dominance relationship between individuals. If they were of the same age class then dominants won (i.e., extracted a final retreat from the opponent) significantly more fights than subordinates (15/18 fights, Binomial test, $p < .01$). Likewise, when opponents were from different age classes, dominants won significantly more fights than subordinates (53/62 fights, Binomial test, $p < .001$). In five additional fights between different age classes no winner emerged. These results do little more than confirm that dominance in an agonistic context (supplanting) extends to another social context (RU fights). Thus, the question of reversals in RU fights was addressed in another way using multivariate analysis in order to take account of variation across all behaviour units employed. It was as-

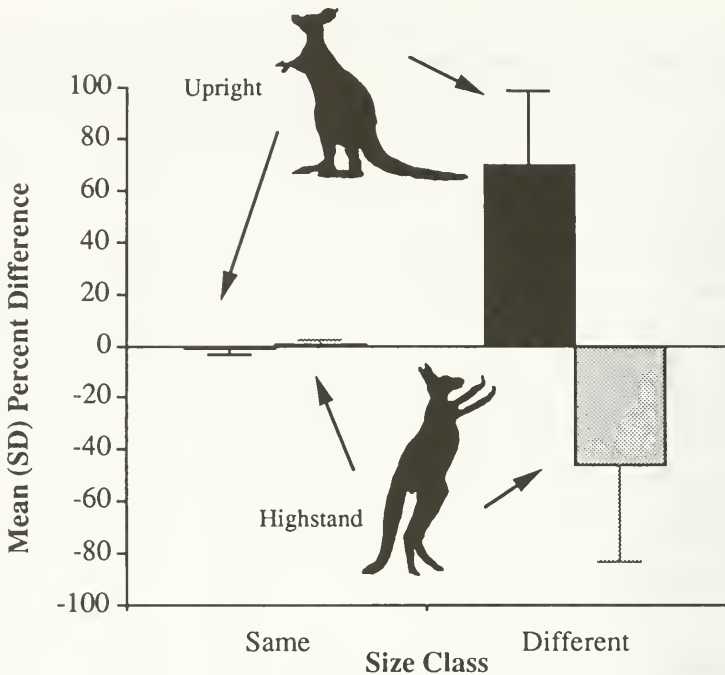


FIGURE 4. Relative durations of dominant and subordinate adopting upright or highstanding postures when they were of the same or a different size class.

sumed that the alpha-male's (M1) behaviour in fights typified the dominant strategy and that the gamma-male's (M8) behaviour typified the subordinate strategy. The behaviour of these two males was then used to classify the strategy employed by all other males in fights using a discriminant analysis (SPSS Inc., 1986). The data on frequency of behaviour units employed in RU fights were used but since the repertoire was large (25 units), the number of variables was reduced by factor analysis (SPSS Inc., 1986) before performing the discriminant analysis. The factor analysis extracted ten factors explaining 70% of the variance and the factor scores on these ten factors were used in the discriminant analysis. The resulting discriminant function correctly classified the fights of the alpha ($n = 17$) and gamma ($n = 23$) males. The function was then used to classify the remaining 130 fights as being either typical of the dominant or subordinate class and this classification was compared to the actual status of the individual performing the behaviour. Reversals were found for some individuals but a dominant was significantly more likely to behave as a dominant (60/85 fights, Binomial test, $p < .001$) than a subordinate and likewise subordinates behaved as subordinates (71/85

fights, Binomial test, $p < .001$). The assumption of a dominant/subordinate role in fights was not random (Kolmogorov-Smirnov, $p < .01$). In the majority of fights (49/85), the opponents assumed the correct dominant/subordinate roles. A reversal of these roles was rare (6/85 fights) but opponents commonly both assumed the same role (30/85 fights).

Partner Selection

The structure of RU fights suggests that individuals do not participate solely to exercise their dominance over another individual. Dominants self-handicap and opponents commonly behave in the same role whether dominant or subordinate. The red kangaroos invest time and energy in fights and may risk injury and, in the field, become more conspicuous and less vigilant to predators. Hence, it is fair to assume that this behaviour is advantageous to the participants. Various theories about the function of play predict that maximum benefits accrue when skills and physical strength are matched to maintain a stable play relationship (Fagen, 1981). Partner selection in 127 fights in the captive population was examined to look at such relationships.

The captive population contained four size classes of males. The frequency of fights between individuals of the same size class (26), or one (87), two (13), or three (1) classes smaller/larger was significantly different from those expected from the distribution of size class differences in the population (Kolmogorov-Smirnov, $p < .001$). The standardized residuals (SR) show that fights within the same size class were about as frequent as expected (SR = 1.89, ns). Fights with a partner one size class smaller or larger were significantly more frequent than expected (SR = 4.31, $p < .001$) but where the size class difference was two or three, fights occurred significantly less than expected (SR = -3.83, $p < .001$; SR = -4.01, $p < .001$; respectively). Thus partner selection tends to bias the outcome in favour of a superior opponent but as this disparity increases then fights become rare.

Partners may or may not derive equal benefits from fights. One opponent may exploit and bully the other or their relationship may be cooperative and beneficial to both. The relationship between kinship and fight partner selection was examined to illuminate these alternatives. The captive population comprised three classes: non-relatives, half-sibs and full-sibs. Fights with non-relatives were significantly more common ($n = 75$, SR = 2.54, $p < .01$) and those with half-sibs significantly less common ($n = 22$, SR = -2.59, $p < .01$) than expected, whereas those with full-sibs were about as common as expected ($n = 30$, SR = -0.52, ns). However, this result is confounded by possible size differences between partners which, as shown above,

significantly influenced partner selection. Even so, the same result holds for fights between opponents of one size class difference: non-relatives ($n = 58$, $SR = 2.47$, $p < .01$), half-sibs ($n = 3$, $SR = -4.05$, $p < .001$) and full-sibs ($n = 26$, $SR = 0.85$, ns). The trend was similar for other size class differences, but sample sizes were too small for robust statistical analysis.

Disruptions and Takeovers

One benefit of these RU fights may be to increase the skills and/or physical development of one or both partners. Therefore, it should be advantageous for a superior individual to disrupt this skill/physical development in a lower ranking individual which may later challenge its dominance status, or, to join in and so match skill/exercise increments. Likewise, more support may be given to the development of a close relative than to an unrelated individual. These possibilities were investigated by analysing fights where disruptions or takeovers occurred by a third individual. A disruption was defined as the intercession of a third individual into a RU fight between two opponents causing that fight to conclude abruptly. A takeover was defined as the displacement by a third individual of one of two opponents engaged in a RU fight followed by immediate initiation of a fight by that individual with the remaining opponent.

Most RU fights (72%) proceeded without a third individual interceding. Where fights were disrupted, the victim was significantly more often of lower than of higher rank to the intruder (14/16 observed, 7/16 expected; Kolmogorov-Smirnov, $p < .001$). Similarly for takeovers, the individual excluded was significantly more likely to be of lower rank to the intruder (19/20 observed, 8.5/20 expected; Kolmogorov-Smirnov, $p < .001$). Analysis at the individual level was not possible with the low frequencies observed but the alpha male interceded in 50% of the fights disrupted or taken over. An individual was more likely to stop the fighting of a non-relative ($n = 26$, $SR = 1.61$) than a half-sib ($n = 13$, $SR = -0.52$) or full-sib ($n = 9$, $SR = -1.34$) but these differences were not significant (Kolmogorov-Smirnov, ns).

DISCUSSION

Fagen (1974) has divided the various approaches to the study of animal play into structuralist and functionalist camps. The structuralists maintain that play can be differentiated from 'serious' behaviour by its form. The most distinctive feature is usually a play-signalling behaviour. Red kangaroos engage frequently in fights

where no resource is in immediate contest and the form of these RU fights suggests that they are play-fighting. The behaviour is most common between younger males and between mothers and their male young, as found in other sexually dimorphic species (Symons, 1978), but is not confined to the juvenile phase. It is differentiated from RR fighting during conflict for a resource (specifically water) by its longer duration, and the absences of threat behaviour and damaging kicks. The latter two are the more distinctive characteristics since RR fighting for access to oestrous females may also be lengthy (Croft, 1981). Initiation of a RU fight may be a simple approach of one male to another, but both males often face each other and engage in grooming and scratching behaviour. They may mirror each other in these actions which, although they are not structurally different to grooming in other contexts, may serve to signal an intention to play without confusion with threat postures.

The tactical goal in RU fighting is to force the opponent off balance with vigorous pushing thus gaining a superior position to force it to retreat. Such goals are characteristic of play-fighting in other mammals (Symons, 1978). In general, the fighting behaviour shows many of the structural features considered to be distinctive in animal play (Bekoff, 1978). There is some lack of dominance distinctions, self-handicapping by the larger of two opponents occurs, threat behaviour characteristic of serious fights is absent, and potentially damaging behaviour is restrained. Thus, the context, the goals, and the structure of RU fighting all suggest that it is a form of play in red kangaroos.

Functionalists maintain that play can be differentiated from other behaviour only if it can be shown to be goal-directed and adaptive. Four functions that have been favoured are assessment, skill development/exercise, regulation of development rates, and socialization (Fagen, 1981).

Assessment is a mechanism for informing individuals of their relative fighting abilities and dominance ranks. In a relatively closed social system, such assessment will be applied to particular individuals. If kinship is recognised then two strategies might emerge. Firstly, if a play relationship is formed between unrelated individuals and results in an increase in fitness then each individual should behave selfishly to emerge dominant in the fight. A loser should stop fighting or attempt to injure its opponent. Secondly, for related play partners the strategy may be to accept the subordinate role and not injure a sib as that could decrease inclusive fitness. These two strategies do not clearly emerge in red kangaroo RU fighting. Partners are moderately different in size and unrelated more often than if they were chosen at random. Thus, the larger individual may be bullying an unrelated smaller one and thus reducing its chances of usurping

its dominance rank. Even so, the smaller individual may gain some benefit by testing itself against a superior opponent ranked above it. There was no evidence that either partner attempted to injure the other although kicking by the subordinate could fall into this category. However, if this kicking were to inflict injury then the dominant would not be expected to accept this fatalistically without severe retaliation. Some cooperation does occur in these RU fighting relationships in that the dominant handicaps itself but perhaps it could thereby be deceiving the subordinate as to its true abilities.

I favour assessment as being an important function of RU fighting in red kangaroos. In the wild, they have an open social system with little group stability and dispersal of males over long distances (Croft, 1981). Thus, assessment of other males' fighting abilities must be generalized rather than specific to certain individuals and this may explain why RU fighting as a form of play continues into adulthood. It may provide assessment with a low risk of injury as opposed to full confrontation in a potentially injurious fight. The results of this study provide no clear relationship between kinship and play partner selection or play behaviour. In an open social system this is probably unimportant. Only one young is reared in a year and so there is no litter-mate, and dispersal makes inbreeding unlikely.

Skill development is a likely outcome of play-fighting. It should improve the coordination of young individuals and the development of winning tactics. However, skill development alone does not explain why red kangaroos continue to play-fight throughout their life. In adulthood, learning about the skills of an opponent rather than learning and improving one's own skills would likely be more important.

Like skill development, exercise is an inevitable consequence of a rigorous activity such as play-fighting. Keeping the cardio-pulmonary and muscular systems in tone could therefore be a benefit of play-fighting. Generalized locomotory activity could serve a similar function without recourse to the complexities of interactional behaviour. Thus, exercise is no doubt a benefit of RU fighting but probably not the only benefit, and RU fighting is probably not the only way to gain the necessary exercise.

Socialization as a function of play implies the establishing and strengthening of social bonds and social cohesion through play behaviour. In red kangaroos where little group cohesion is evident this is unlikely to be an important function of play-fighting. As stated above, relationships are probably generalized to particular classes of individuals rather than specific known ones. This functional hypothesis has also been discredited because of its group selectionist connotations (Fagen, 1981).

Play-fighting in red kangaroos is neither truly cooperative nor disruptive and selfish. Fagen (1981) drew a similar conclusion in re-

viewing animal play in other species. As Fagen points out, the interests of play partners will rarely coincide. Each has its own requirements for experience in play and so a stable relationship will only form where there is some compromise between the partners' differing optima. Self-handicapping, lack of dominance distinctions, and role reversal are reflections of this. The darker side of red kangaroo play-fighting is expressed in the disruption of play-fights by a third interceding individual. Here it was shown that dominants, particularly the alpha male, reduce the play-fighting of lower ranks to some extent. This bullying may be to the higher ranked individual's advantage in delaying usurpation of their rank from below in the hierarchy. A corollary of this observation and the assessment hypothesis is that an alpha male in decline from age-related disabilities or injury should avoid play-fights with the lower ranks. Rejection of play-fight invitations were too infrequent in this study to analyse this. However, some observations on an eastern grey kangaroo (*Macropus giganteus*) group were also made at the Cowan field station (Croft, unpubl.). The alpha male in that group avoided fights with the beta male whenever the latter approached with invitational behaviour. Shortly after these observations, the beta male attacked the alpha one causing fatal injuries.

The 'boxing' behaviour of kangaroos intrigued and delighted the early European observers of the Australian fauna (e.g. Dahl, 1897). Man-kangaroo matches were an occasional diversion for the early colonists (Hornage, 1972). This study shows that these boxing matches in red kangaroos fulfill an important role in their social organization and should neither be viewed as potential death matches nor dismissed as human amusement. If we reflect on the consequences of our own school yard brawls, it is evident that play-fighting has an important influence on status and social development. In a sexually dimorphic species such as the red kangaroo, where competition between males for matings is intense, development and improvement of fighting skills and assessment of potential competitors will be important. Play-fighting provides an avenue for this without the high risks of injury in an escalated confrontation where kicks are the cut and thrust of the fight rather than a simple parry.

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